

CHAPTER ONE

Community Ecology Lives

Understanding what controls the structure and diversity of ecological communities has invoked the intellectual Prepower of ecologists since at least the time of Charles Darwin (1859, p. 125).

In the case of every species, many different checks, acting at different periods of life, and during different seasons or years, probably come into play; some one check or some few being the most potent, but all concurring in determining the average number or even the existence of the species. . . . When we look at the plants and bushes clothing an entangled bank, we are attempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!

Few conceptual undertakings in science, much less ecology, have such an ambitious goal that applies over such a wide range of scales in space (May 1988; Wilson 1992; Lawton 1999). Community ecology is difficult because, as Darwin recognized, many factors affect the existence and abundance of organisms. Ecologists now have explored in detail how resource availability, disturbance, dispersal, predation, disease, mutualism, evolutionary history, scale of observation, and variability of physical conditions and resources over space and time (heterogeneity) affect community structure. These different factors influence community structure at different scales in space and time. Simberloff (2004) has suggested there are few general principles; the goal for now should be the accumulation of case studies until we can understand the context of different outcomes of community organization. Even more pessimistically, Lawton (1999) suggested that we Òmove onÓand essentially give up on a general theory, given that communities seem to have highly contingent, unpredictable patterns.

Different scientific approaches to understanding community structure emerged early in the development of ecology as a science (Kingsland 1988). Ecologists use a deductive approach to predict community structure from particular mechanisms, such as competition for resources or dispersal (Tilman 1982, 1994; Belovsky 1986; Hubbell 2001; Chase and Leibold 2003). Ecologists adopting this approach often develop analytical, mathematically derived hypotheses of interactions among species. These predictions are most often compared with the results of laboratory and field experiments. The other approach is more inductive, in that ecologists explore patterns in community structure and compare them with broad, often non-mathematical, hypotheses that do not specify the mechanisms generating such patterns. Each approach has provided major advances and insights (Brown 1981, 1995; Huston 1994; Ricklefs and Schluter 1994; Rosenzweig 1995), but they remain largely unreconciled. The difference in these two approaches has separated ideas and data whose synthesis might lead to a more thorough understanding of community structure. To move forward, both deductive and inductive approaches must be synthesized.

In this book, I propose a new framework for predicting the structure and diversity of ecological communities that might help synthesize previous theory and data. This framework emerges out of incorporating two critical elements of the inductive approaches, scale and heterogeneity, into the analytical mathematical formalism of the more deductive approaches. The new framework makes novel predictions of diversity that depend explicitly on the spatial and temporal scale of the observer, the inherent heterogeneity of the environment in space, and the scale of response to the environment by different species in space. It is a formal extension of the original ideas of environmental and perceptual "grain" introduced by Levins (1962, 1968) and MacArthur (1972).

The emphasis on scale and heterogeneity requires a tool that can simply describe the complex physical structure of nature: fractal geometry. Fractal geometry assumes that distributions of physical material and conditions and/or biological organisms in the environment are statistically similar across a range of meaningful spatial scales (Mandelbrot 1982; Milne 1992). In that sense, it is a "neutral" model of heterogeneity. It describes very complex-looking distributions with simple mathematical scaling laws. By inserting these scaling laws

directly into classical population dynamics models, new models emerge that incorporate the scale-dependent description of spatial heterogeneity so critical to the interpretation of macroecological patterns (Brown 1995). Just as importantly, these models can only be interpreted in terms of the spatial scales of the species involved. By assuming that organism body size provides a first approximation to these scales (Peters 1983; Calder 1984; Charnov 1994; West et al. 1997; Brown et al. 2004), the models explicitly link the conditions for coexistence to species body size (Morse et al. 1985) and thus to species composition, abundance, and diversity. The utility depends on including both scale and a metric of spatial pattern in traditional models of resource dynamics and consumption. The approach would apply even to the many environments in which spatial patterns appear to vary across scales (Allen and Holling 2002), as the scaling laws inherent in the fractal geometric description of heterogeneity can be adapted to include exponents that are themselves functions of scale. For the purposes of this book, I devote my attention to how a simple assumption of fractal geometry, as a first approximation, can elucidate how species select and partition packages of the same limiting resource in order to coexist.

WHY ARE THERE SO MANY SPECIES?

To understand how such a framework might provide progress and synthesis, I return to 1959, when G. Evelyn Hutchinson posed the question, "Why are there so many species?" This deceptively simple question was novel then because the results of the previous century of natural history, ecological theory and experimentation led to a conundrum. Theory (Lotka 1925; Volterra 1926) and laboratory experiments (Gause 1934; Park 1948) suggested that coexistence occurred only under special conditions. The interpretation of these results led to the "principle of competitive exclusion" — no two species that are identical in their use of resources can coexist, and coexistence therefore occurs only under special conditions (Hardin 1960). However, this "principle" made little sense to natural historians, who confronted it with the observation of myriad coexisting species, many of which seemed to use similar resources (Elton 1958; Hutchinson 1957).

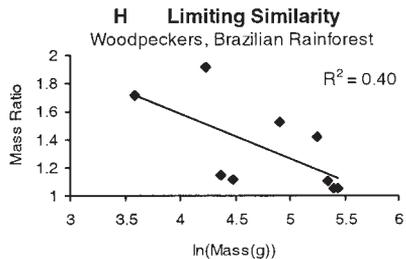
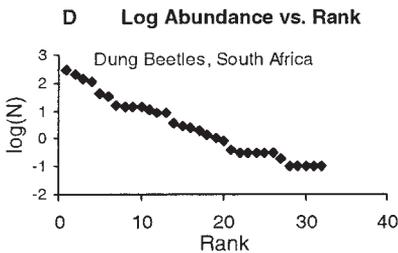
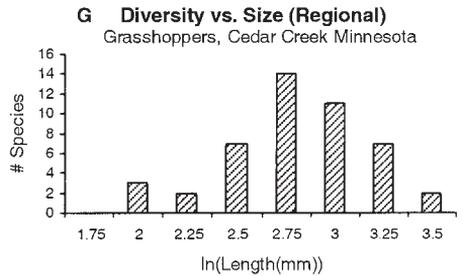
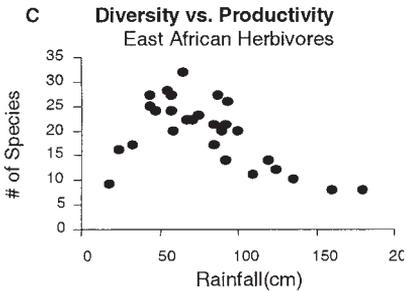
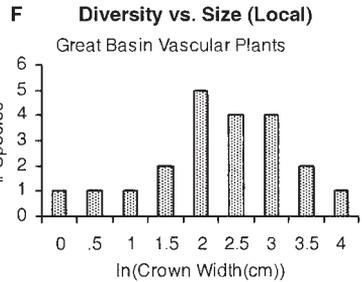
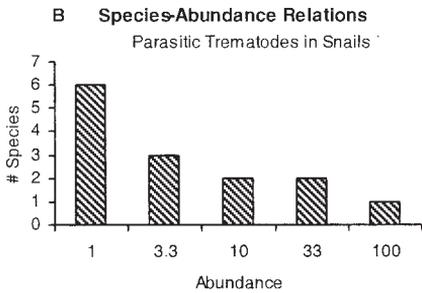
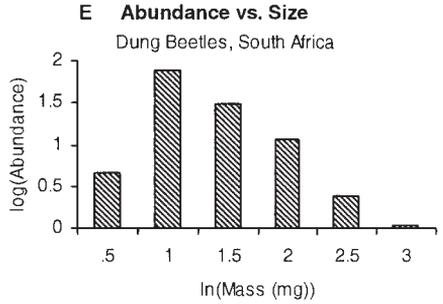
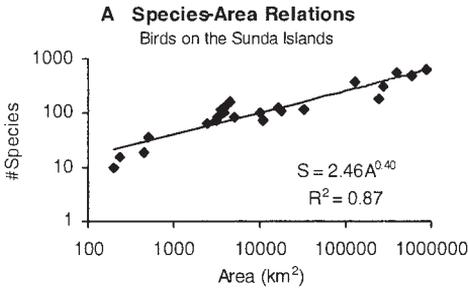
Hutchinson's question challenged the principle of competitive exclusion, and thus challenged theoretical and experimental ecologists to determine how different species must be to coexist, and how these differences determine the large, but not infinite, number of species we observe in nature. Ecologists addressed this challenge in two major ways. First, population ecologists began the search for potential mechanisms that could allow multiple species to coexist on relatively few (or a single) limiting resources. Differences in diet overlap were interpreted as leading to differences in per capita competitive effects. When placed in classical Lotka-Volterra models, these per capita effects among all possible species pairs ultimately predicted a community matrix of interaction coefficients among multiple species (MacArthur 1970; Strobeck 1972; May 1976). Such differences in diet overlap among species were thought to emerge from the evolution of different optimal foraging strategies (MacArthur and Pianka 1966; Emlen 1966; Schoener 1971) in which individuals selected diet items to maximize fitness. Species would have different optimal diets, which would not completely overlap and therefore would promote their coexistence. Other work showed how pairs of species might coexist only when they differed in the size or type of resources used (MacArthur 1972; Schoener 1974; Tilman 1982). In contrast, MacArthur and Wilson (1967) suggested that species diversity in islands or fragmented habitats were controlled by colonization and extinction. All these approaches focused on how community structure emerged from the dynamics and evolution of populations near equilibrium population sizes, as dictated by competition with other species. Natural selection, when combined with competition, could yield differences among species in their morphological, physiological, and behavioral traits. These trait differences would allow them to use different *niches*, or combinations of physical locations, conditions, resources, and interactions with competitors and predators, thus promoting coexistence (Grant 1986; Thompson 1994; Leibold 1995; Chase and Leibold 2003). A comprehensive theory of the niche and the role of niches in predicting community structure dominated ecological thought by the late 1970s and provided a structure for interpreting a tremendous volume of natural history information.

Despite this progress, the population dynamic approach to community ecology could only vaguely predict the wealth of patterns in

species abundance and diversity, particularly at larger spatial scales. This void was filled by community ecologists, who employed a more inductive approach. For example, Preston (1962) and MacArthur (1965) found predictable patterns in the abundance and diversity of different-sized species in communities. These results inspired other ecologists to search for patterns in other taxa and environments. Numerous studies yielded relationships between species diversity and the area of continents and islands, and relationships between diversity and productivity (Whittaker 1975), disturbance (Connell 1978), latitude (MacArthur 1965), and various measures of resource and habitat heterogeneity (e.g., MacArthur 1965). These patterns largely were explained by a myriad of verbal hypotheses or statistical models (Brown 1995; Rosenzweig 1995).

By the late 1970s, mainstream theoretical ecology and the search for biogeographical patterns of community structure had converged in two areas. One was related to species-body size. Mathematical models of competition and coevolution predicted that a species-body size should constrain its ability to coexist with other species. Competing species might show a striking regularity: there might be a limit to how similar in size species could be and still coexist (MacArthur 1970). This was qualitatively confirmed by the patterns in species-body size observed in many communities (Hutchinson 1959; Hutchinson and MacArthur 1959; Cody and Diamond 1975). The other was the development of island biogeography theory (MacArthur and Wilson 1967; Simberloff and Wilson 1969), based on the idea of dispersal limitation and local extinction of species. This theory was applied to understand community patterns on islands and fragmented habitats on continents (see Rosenzweig 1995). These areas of convergence suggested that further development of mathematical models of competition, coevolution, and colonization and extinction dynamics might produce a synthetic theory of community structure. Such a synthesis would be able to simultaneously explain the major patterns of species diversity and abundance, how these patterns incorporate the structure of species with different body size, and how they change with the scale of observation (see Fig. 1.1 for some examples).

Synthesis would wait at least another twenty years. In the early 1980s, community ecology took a dramatically new turn. The predictions of theory had far outstripped experimental evidence from the



Beld. Although the population dynamical models of community structure could be used to interpret Beld data, alternative models that did not invoke species interactions and evolution could predict some of the same patterns. For example, body size patterns in communities were sometimes equally well predicted by Null models (Simberloff and Boecklen 1979) of species with randomly assigned body sizes. This continues today with models in which species traits do not determine their abundance (Hubbell 2001; Harte et al. 2005, 2008). Moreover, ecologists began to question whether communities were ubiquitously structured by competition or contained populations anywhere near population equilibrium (Lawton and Strong 1981). They argued that other interactions, such as predation or mutualism, or mechanisms such as colonization limitation and local extinction, might be just as important in structuring communities. These questions spawned a flood of Beld experiments to determine the prevalence of competition, predation, and other interactions within communities (Connell 1983; Schoener 1983; Sih et al. 1985). After two decades, these studies illuminated complex food webs comprising dozens of direct species interactions and even more indirect ones (Paine 1992; Wootton 1997). Communities appeared to defy any simple mathematical description, such as a

FIGURE 1.1. Examples of patterns in community structure that should be able to be predicted by ecological theory from mechanisms of species coexistence, dispersal/colonization limitation, or neutral theory. (A) Species-area curve for all bird species on the Sunda Islands (MacArthur and Wilson 1967). (B) Species richness-abundance relationship for trematode parasites of the marine snail *Corithidia californica* (Lafferty et al. 1994). (C) Species richness vs. rainfall, a surrogate of productivity, for mammalian herbivores >300 g in 28 preserves in Kenya and Tanzania (Ritchie and Olff 1999). (D) Log abundance vs. species rank in abundance for savanna dung beetles on sandy soils (Coleoptera) in Mkuzi Preserve, South Africa (Doubé 1991). (E) Log abundance vs. body mass (mg) for savanna dung beetles on loamy soils in Mkuzi Preserve, South Africa (Doubé 1991). (F) Species richness of vascular plants in the Utah Great Basin vs. size (maximum width of canopy/stem) in a 10 x 10 m plot (Ritchie and Olff 2005). (G) Species richness of grasshoppers (Orthoptera: Acrididae) found at Cedar Creek Natural History Area, Minnesota (20 km²) (Ritchie 2000). (H) Limiting similarity in a guild of tropical forest woodpeckers, where mass ratio is the ratio of masses (larger: smaller) of adjacent-sized species vs. the size of the larger species in each pair (Terborgh et al. 1990).

community matrix of pairwise species interaction coefficients that would determine the equilibrium abundances of species. Instead, they seemed to require complex combinations of non-linear equations to describe their dynamics (Abrams 1988; Schmitz 1992; Leibold 1996). Even simple 3-species combinations had rich dynamics that exhibited cyclic or even chaotic behavior (May 1976; Huisman and Weissing 1999, 2001). The vision of predicting community structure and its major patterns in any general way was all but abandoned by most ecologists.

A FOUNDATION FOR SYNTHESIS

Despite the much-needed focus on field experiments over the past 20 years, many important conceptual developments during this period provide renewed optimism for a synthesis in community ecology. The application of hierarchy and complexity theory to ecology (Allen and Starr 1982; O'Neill et al. 1986; Allen and Hoekstra 1992) suggests that communities are too complex to be understood through the traditional approach of using differential equation models for each species's population dynamics. Recent neutral models of community structure (Hubbell 2001; Bell 2001; Volkov et al. 2003; Alonso et al. 2006; Harte et al. 2008) suggest that certain spatial patterns can result from simple processes in space and time that do not depend on species traits. Ecologists also now increasingly recognize that many patterns in ecology change with the scale at which they are observed (Greig-Smith 1983; Wiens and Milne 1989; Levin 1992; Kunin 1998). Studies of interactions among plant species suggest that underlying trade-offs in the advantages of different physiological and morphological traits can explain species coexistence (Grime 1979; Tilman 1988; Berendse et al. 1992; Leibold 1989, 1996). New studies of how species's traits scale with body size (Peters 1983; Calder 1984; Charnov 1994; West et al. 1997; Enquist 2001) suggest that such trade-offs may depend generally on the body size of organisms. Some experimental field studies of terrestrial herbivores find that in fact species may be more likely to coexist than expected because trait differences confer access to exclusive resources (Schoener 1976; Belovsky 1986, 1997; Ritchie and Tilman 1993; Chase 1996; Ritchie 2002). These studies suggest that a species's ability to

coexist is driven more by the amount of its exclusive resources than by its competitive ability for overlapping or shared resources. Finally, the recognition that much of nature exhibits fractal geometry (Mandelbrot 1982) provides a potentially powerful tool for incorporating scale and heterogeneity into models of community structure (Morse et al. 1985).

These seemingly disparate developments point to a potential revision in understanding community structure and diversity. Multiple differential equation models of consumer–resource interactions, one for each species, can generate the coexistence of many species (Huisman and Weissing 1999, 2001; Brose et al. 2004), but this approach seems unlikely to be useful in generating general predictions. The next best option perhaps is to focus on trade-offs in the advantages of species traits (Tilman 1990) and their potential for generating exclusive resources (Belovsky 1986, 1997; Ritchie 2002). Although there are many studies of trade-offs and coexistence (Sommer and Worm 2002), what is still missing is the connection of these traits to the distribution of resources in the environment, observed at different spatial scales (Levin 1992). More specifically, *how do species with different traits exploit biotic and environmental heterogeneity, how does this exploitation change with scale, and how does this allow coexistence?*

In this book, I develop a model to account for how species that are limited by the same resource might coexist. Specifically, I develop models to account for how community structure might be influenced by spatial and temporal heterogeneity in the distribution of habitat and resources across a range of scales of observation. The key assumptions of the model are:

1. potentially coexisting species all consume the same resource (MacArthur 1969; Tilman 1982);
2. individual organisms sample the environment at some characteristic scale or grain size that likely corresponds, on average, to a species' body size (Levins 1962, 1968; MacArthur 1972; Wiens and Milne 1989);
3. most organisms must consume some other material, which I call food, in order to acquire resources;
4. resources and habitats have a fractal-like heterogeneous distribution over some range of scales of observation (Milne 1992, 1997); and

5. individuals will select clusters of resources in a way that maximizes their fitness for a given distribution of resources and habitat (MacArthur and Pianka 1966; Emlen 1966; Schoener 1971; Charnov 1976; Stephens and Krebs 1986).

By applying these assumptions, some of which are based on some long-held ideas in ecology, to a classical model of the dynamics of a consumer species and its resource, I develop the mathematical background to describe the fundamental process of resource consumption in a heterogeneous environment. As I will show in the ensuing chapters, fractal geometry provides a neutral description of heterogeneity, that is, the pattern of heterogeneity is similar across scales of observation. However, *when fractal distributions are sampled with different grain sizes, the density and cluster size distributions of resources become explicitly dependent upon the scale of observation and measurement.* Emerging data (Johnson et al. 1996; Halley et al. 2004) suggest that fractal geometry provides a first-order approximate description of spatial distributions in nature that is certainly better than assuming random or uniform distributions (Tilman 1982; Tilman and Wedin 1991). David Morse and John Lawton (Morse et al. 1985) provided a hint of the potential of fractal geometry to address problems of resource availability and community structure (May 1988), and this idea has developed over the last decade (Milne et al. 1992; Palmer 1992; Ritchie 1997, 1998; Ritchie and Olff 1999; Olff and Ritchie 2002; Green et al. 2003; Halley et al. 2004).

The resulting model predicts the following. Species with different sampling scales (grain size) should be selective for different resource cluster (patch) sizes. An optimal minimum resource cluster size, or giving up density, increases with sampling scale according to a simple scaling law. This minimum defines a niche boundary along a gradient of resource cluster sizes that ultimately determines whether a species can coexist with others. I test these predictions with results from several sets of data on minimum resource cluster sizes accepted by dung beetles, item sizes selected by mammalian and insect herbivores, and seed sizes and seed patch densities selected by desert granivores.

When resources are imbedded in another material (food: plant tissue, animal tissue, organic matter, water) that must be consumed, species with different sampling scales experience a trade-off in their optimal

minimum food patch sizes and within-patch resource concentrations (Ritchie and Olff 1999). This trade-off depends fundamentally on heterogeneity, as it disappears when resources are random or homogeneous. This trade-off predicts the maximum, minimum, and optimal sampling scales for a guild of species that use the same resource, as well as their abundances and a limit to the similarity in sampling scales among species. Species of different sampling scales coexist because they have exclusive use of particular sets of food patch sizes and resource concentrations. To the extent that body size provides a first approximation to grain size, the model therefore predicts the number and abundance of species of different size that can coexist. Thus, the structure of a community can be predicted from the likely body sizes that would sort via competitive dynamics to allow the maximum number of species to persist. This predicted structure results independently of the detailed population and competitive dynamics of species, but is sensitive to environmental factors such as area, habitat fragmentation, and productivity. I then test the predicted patterns in species body size similarity, maximum and minimum body size, species abundance, and species richness with data from many different guilds including mammals, birds, plants, arthropods, and marine zooplankton.

The resulting model yields a framework, based on population dynamics and evolution in a heterogeneous environment, for predicting major patterns of community structure. Because of its explicit inclusion of factors such as productivity, habitat distribution, and scale of observation, this framework can potentially be used to evaluate the consequences of environmental change, such as habitat loss, for community structure and biodiversity. As such it provides a niche-assembly-based model of community structure and species diversity that predicts multiple patterns that can be directly compared with those of alternative theories such as neutral theory (Hubbell 2001; Harte et al. 2008) or the storage effect (Chesson 1994, 2000).

I finish the book by placing this model in the context of other community structuring mechanisms such as colonization/extinction dynamics, disturbance, predation, and environmental constraints such as temperature. I also recognize that many large-scale patterns of community structure and diversity include all species in a taxon, regardless of resource guild. Clearly these patterns result from combining the structure of their subcomponent guilds, and thus from the law of large

numbers. However, because the model predicts the maximum, minimum, and optimum sizes of each guild, it can predict constraints on the diversity patterns for a collection of guilds. I explore these predictions and their support by field data to show how the traditional species patterns of community structure may emerge as the conglomeration of local, guild-specific patterns predicted by the deductive approach I present in this book.

This theory, if ultimately supported by field experiments and more data, furthers the original goals of the early community theorists, who perceived links between organism size, selective foraging, niche boundaries, and competitive coexistence. Because the model brings together several ideas in a novel way (scaling, fractals, exclusive resources, foraging for food rather than resources directly), few if any of its qualitative predictions have been tested experimentally. Thus, evidence from observed field data to support the predictions of the model is circumstantial for now. Other theoretical models, such as the neutral theory of biodiversity and biogeography (Hubbell 2001; Alonso et al. 2006) or spatial macroecology (Ostling et al. 2003; Green et al. 2003; Harte et al. 2005, 2008) suggest that trait differences among species do not determine community structure, and might in some cases explain observed data just as well, if not better, than classical niche models. Since mechanism can seldom be inferred from pattern, I suggest ways that the trait-dependent, niche assembly processes of resource competition might provide direct alternative predictions of the same types of patterns. The idea that multiple processes may simultaneously structure communities is not new (MacArthur and Wilson 1967; MacArthur 1972; Tilman 1994), but the development of a niche-based theory that predicts a full range of community patterns means that an explicit theory of combined niche and dispersal assembly may not be far away (Marquet et al. 2007).

This book in many ways rejuvenates a classic paradigm (Simberloff 1983): the composition, diversity, and abundance of species can be understood from their differences in morphology, behavior, and physiology (MacArthur 1972). Rather than moving on (Lawton 1999) to view community ecology as an amalgam of contingent and unpredictable interactions and processes (Simberloff 2004), this book provides optimism for community ecology. We know much more about how the morphology, behavior, and physiology of individuals influence inter-

actions with the environment and among species, as witnessed by literally hundreds of studies of species interactions and their modification by the traits of species. The ideas inherent in the original formal development of niche theory and community structure in the 1960s and 1970s are brought back in this book because they are very useful at synthesizing the influence of species traits on their interactions with the environment and other species. In particular, the book re-emphasizes body size as an axis of niche differentiation and extends this concept into an explicit theory of species abundance and diversity. Moreover, the incorporation of scale and heterogeneity, by using the new abstraction of fractal geometry, enlivens these classical niche-assembly ideas so that they can explain many patterns of community structure in unprecedented ways. The book is therefore far from a dusting off of classics; rather it represents a new and potentially powerful solution to a classical problem.

SUMMARY

1. Ecologists need to be able to predict multiple patterns in community structure from mechanisms that govern interactions among species in specific habitats across a wide range of spatial scales (experimental plots to continents).
2. I propose a new model for predicting the structure and diversity of ecological communities that incorporates two critical elements of diversity: scale and heterogeneity, into an analytically mathematical form.
3. As a first useful step, the new framework will use fractal geometry to simply describe heterogeneity in resource distributions in an explicitly scale-dependent way.
4. The resulting model will predict the existence and boundaries of exclusive niches for species with different sampling scales that use the same heterogeneous resource, and the limit to how similar such species can be and competitively coexist.
5. To the extent that sampling scale is associated with organism body size, these exclusive niche boundaries will also predict the relative abundance, maximum and minimum size, and diversity of species of different size.

6. The model's quantitative predictions will be compared with many different observed body size and diversity patterns for a wide variety of plant, invertebrate, and vertebrate communities.
7. Although the book will revisit some less popular but classical ideas of niche-based assembly of communities, the new abstraction of fractal geometry enlivens these ideas so that they can explain many patterns of community structure in unprecedented ways.